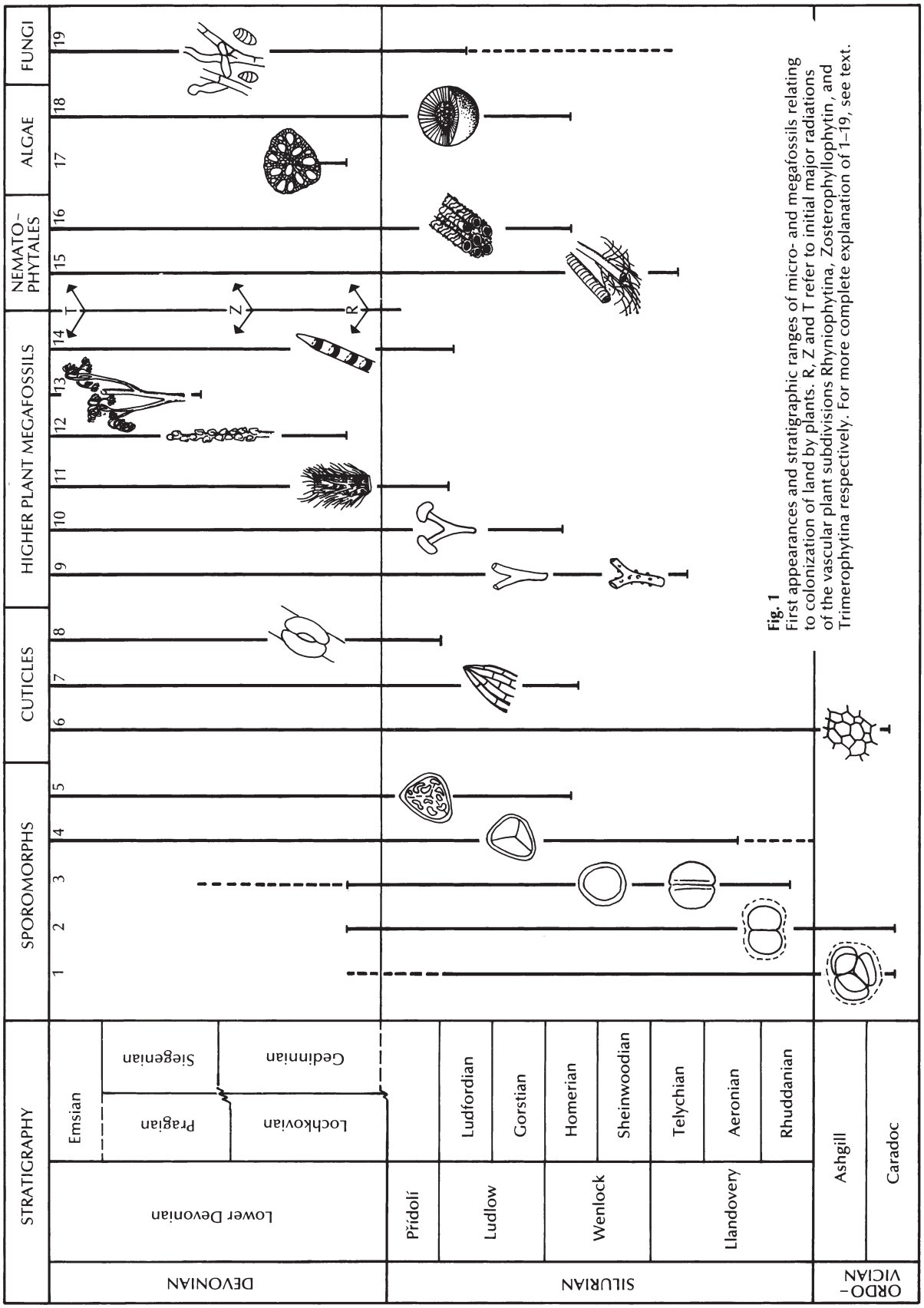
STRATIGRAPHY
SPOROMORPHS
CUTICLES
HIGHER PLANT MEGAFOSSILS
NEMATO-PHYTALES
ALGAE
FUNGI
DEVONIAN
SILURIAN
ORDO-VICIAN
Lower Devonian
Emsian
Siegenian
Gedinnian
Pragian
Lochkovian
Přídolí
Ludlow
Ludfordian
Gorstian
Wenlock
Homerian
Sheinwoodian
Llandovery
Telychian
Aeronian
Rhuddanian
Ashgill
Caradoc
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19
T
Z
R
Fig. 1
First appearances and stratigraphic ranges of micro- and megafossils relating to colonization of land by plants. R, Z and T refer to initial major radiations of the vascular plant subdivisions Rhyniophytina, Zosterophyllophytin, and Trimerophytina respectively. For more complete explanation of 1–19, see text.

obscure, as vascular tissue has never been demonstrated.

4, 5. Monads with triradiate marks. The earliest monads not derived from obligate tetrads are smooth walled, usually with equatorial thickening, e.g. *Ambitisporites* which is later recorded in Přídolí *Cooksonia pertoni* sporangia. Sculptured monads occur continuously from the Homerian, showing rapid diversification and increases in numbers in the Ludlow and Přídolí. For the most part their origins, be they bryophyte or tracheophyte, are unknown, but their presence in Silurian and Gedinnian *Cooksonia pertoni* (Fanning *et al.* 1988) indicates that some of the producers may have been rhyniophytoid (*10*).

Cuticles

6. 'Nematothallus'. Associated with the earliest tetrads are small cuticular fragments, thought analogous to vascular plant cuticles. They lack stomata and are usually imperforate, with smooth ?outer surface. Ornamented forms appear in the Wenlock and continue into the Gedinnian. A reticulate pattern represents the outlines of surface cells in the underlying tissue. In *Nematothallus*, such cells were ± isodiametric in tangential section, while in the cuticles of higher plants they are elongate vertically. Lang (1937) suggested that they covered *Nematothallus*, a thalloid plant composed of tubes which he placed in the Nematophytales (*15, 16*), a taxon for plants with organization neither algal nor higher plant.

While there may be some doubt that all durable spores derive from land plants, this is not the case for cuticles, although being imperforate and hence relatively impermeable to gases, their function and even composition in *Nematothallus* might have been different from that in tracheophytes, e.g. primarily as UV screens, facilitating runoff, or in defence. It is unlikely that they belonged to the tetrad producers because, although the first records are coincident, cuticles persist into the Emsian and are sometimes quite common constituents of Lower Devonian assemblages.

7, 8. Higher plant cuticles. Homerian fragments with larger, more strongly demarcated and aligned cells are interpreted as sporangial from comparison with dispersed and *in situ* Gedinnian rhyniophytoid examples (*10*). Cuticles without stomata deriving from sterile axes occur in the northern hemisphere Ludlow. The earliest *direct* evidence for stomata (with two guard cells) comes from sterile axes at the base of the Přídolí, with examples on *Cooksonia* and *Zosterophyllum* recorded in the Gedinnian. However, since stomata were described on Canadian Emsian *Baragwanathia abitibiense* they were probably also present on the earlier Australian Ludlow *B. longifolia*, where cells are not preserved.

Higher plant megafossils

9. Sterile axes. It is usually accepted that those with dichotomous branching and peripheral support tissues (sterome), the earliest being Llandovery *Eohostimella*, are derived from erect land plants. Late Silurian and early Devonian examples (e.g. *Hostinella*) possess a central strand composed of tracheids (*14*), but whether or not pre-Ludlow representatives were vascular is unknown. Some may derive from plants of small stature in which tracheids had not yet evolved, while others may possess conducting tissues of bryophytic nature (cf. Lower Devonian *Aglaophyton (Rhynia) major* which exhibits many homoiohydric characters, and would be assigned to the Tracheophyta but for the moss-like conducting tissues).

10–13. Fertile tracheophytes. Wenlock *Cooksonia* (Rhyniophytina: *10*) is generally accepted as the earliest erect pteridophyte-like plant (Edwards *et al.* 1983). Reservations as to its affinity stem from a complete lack of anatomy. Spores occur in Přídolí, and stomata and sterome in Gedinnian *C. pertoni*. Tracheids have never been demonstrated in central strands. Thus although *Cooksonia*, *Salopella* and *Steganotheca* are usually assigned to the Rhyniophytina because of general morphological similarity to later examples, e.g. *Rhynia gwynne-vaughanii*, they are better called 'rhyniophytoid' to emphasize our ignorance. A major radiation is recorded in the early Gedinnian, but they then became insignificant constituents of land vegetation (Edwards & Fanning 1985).

Baragwanathia longifolia (*11*) in Australian Ludlow strata is morphologically similar to Lower Devonian examples, with sufficient anatomical as well as morphological characters to indicate lycophyte affinity. Thus, even in the absence of anatomy in Silurian representatives, its vascular status is unquestioned. The earliest lycophyte with typical

sporangium/sporophyll organization is the late Emsian *Leclercqia*.

Zosterophyllum myretonianum (*12*) is the earliest fertile member of the Zosterophyllophytina, although there are records of its characteristic branching (K- and H-shaped) in sterile Přídolí axes. The first major zosterophyll radiation is recorded in the late Gedinnian of south Wales. *Dawsonites* sp. (13), a fragment of a fertile truss of *Psilophyton* in the south Wales Siegenian, marks the beginnings of the Trimerophytina. The Ludlow Australian record is less convincing. The trimerophytes diversified rapidly in the Emsian and are considered ancestral to ferns *s.l.*, progymnosperms and sphenopsids.

Nematophytales

15. Microfossils of tubular organization, either as isolated tubes or wefts, are recorded from the Telychian into the Lower Devonian. The most conspicuous tubes are internally sporadically thickened ('banded'), broadly resembling tracheids in their ornament, but there is no direct evidence that they were lignified. The source plants are problematic: they occur with smaller tubes in *Nematothallus* (Lang 1937) and have been found in plants with organization otherwise typical of *Prototaxites* (*16*). The habitats of such organisms, be they freshwater or terrestrial, remain as conjectural as their affinities. In that some tubes (but not banded forms) have been recorded attached, rather than just adpressed to cuticles of *Nematothallus* (*6*) type, they may well derive from land plants. Further isolated examples include tubes with smooth thick or thin walls, or filaments (occasionally branched) composed of elongate, narrow cells. The latter frequently occur in monotypic wefts or may be associated with wider smooth or banded tubes. Some of the associations may belong to *Nematothallus* or *Nematoplexus*.

16. Prototaxites (Wenlock–Upper Devonian) is included because it is sometimes cited as a land plant largely due to its occurrence in tracheophyte assemblages in freshwater sediments. Its organization, in which narrow filaments enclose wider smooth tubes, is unique, and hence in the absence of reproductive organs its affinities, possibly algal or fungal, remain unknown, and speculation on the functions of its tissues unrewarding.

17. Parka, best known from the Scottish Gedinnian, a possible epiphyte in lacustrine habitats, may have some relevance to the ancestry of higher plants in that it has been compared with the charophycean *Coleochaete*, although the latter lacks the cavities with numerous alete spores found in *Parka*. Comparative biochemical and ultrastructural studies suggest that among the green algae the Charophyceae show closest similarities with bryophytes and tracheophytes while *Coleochaete*, with its parenchymatous organization, and protection, nutrition, and prolonged retention of the zygote, possesses the greatest number of advanced features.

18. Pachytheca is exceedingly common in certain marginal fluviatile and lacustrine facies in the Lower Devonian. Its frequent association with *Prototaxites* has led to the suggestion that it was involved in its vegetative reproduction. However, the fossils suggest that the organism comprised a sphere of a mucilage-like substance in which filaments of cyanobacterial dimensions were embedded. Its habitat is interpreted here as freshwater, possibly littoral lacustrine.

19. Fungi. Although not considered plants, fungi are included here because it has been suggested that initial terrestrialization was possible only after the development of a symbiotic association between a semiaquatic green alga and an aquatic oomycete fungus, and that in the colonization of nutrient-poor environments the fungus would have exploited large volumes of substrate for minerals (cf. mycorrhiza today). Resting spores of presumed mycorrhiza in some Rhynie Chert axes are frequently cited as supporting evidence, but the abundant spheres and hyphae may just indicate saprotrophism (i.e. decomposition of dead organisms) in peat development. Further evidence for terrestrial fungi is the record of ascomycetes remains (hyphae, probable conidia, and ascospores) from the Ludlow of Gotland (Gray 1985), and similar, but more poorly preserved, material from the late Llandovery.

Terrestrial vegetation

It is postulated that moist land surfaces in the early Palaeozoic would have been coated with a green scum, perhaps initially of cyano- and eubacteria, later joined by filamentous and unicellular algae. Such an encrusting layer would have both physically stabilized and chemically broken down the substrate, releasing nutrients and, in stable environments, resulting in the build-up of humus (see also

Section 1.8.1). From the middle Ordovician onwards microfossils morphologically convergent with those from later tracheophytes suggest a novel vegetation, possibly with thalloid organisms covered by cuticle and spore producers with liverwort life-style; aerial dispersal indicates the attainment of some stature. The appearance of *Ambitisporites* in the Llandovery heralded a new phase — the advent of pteridophyte-like plants with axial organization, possibly forming a 'turf' just a few centimetres high. The larger size permitted by homoiohydry, the concomitant maintenance of turgor and hence a hydrostatic skeleton, conferred potential superiority over poikilohydric forms in terms of wind dispersal of propagules and in shading, thus limiting the productivity of smaller forms. Throughout the late Silurian there is an increase in axis diameter and length of fragments: sprawling *Baragwanathia* probably formed thickets. Lower Devonian assemblages suggest that many of the tracheophytes grew in monotypic stands, extensive cover resulting from prolonged rhizomatous activity. Such plants would have provided mutual support — some of the Emsian trimerophytes attained a height of over 1 m. As to habitats, the best direct evidence comes from the Rhynie Chert, but as all these early pteridophytes were homosporous (i.e. with spores of one size), the free-living gametophyte would have required moist conditions both for vegetative growth and reproduction. With regard to route of terrestrialization for higher plants, physiological considerations support transmigration from fresh water on to land.

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1.8.3 Invertebrates

P. A. SELDEN

Introduction

The diversity of invertebrate species on land greatly exceeds that in the sea; this is almost entirely due to the terrestrial insects which form 70% of all animal species alive today. However, of over 30 invertebrate phyla, only the arthropods, the molluscs, and the annelids have significant numbers of macroscopic terrestrial representatives. A greater number of phyla include very few terrestrial species, cryptobiotic representatives, or internal parasites on terrestrial organisms. The body plans of some highly successful marine phyla have apparently precluded their terrestrialization; these include the sipunculid, echiuroid, and priapulid worms, cnidarians, lophophorates, chaetognaths, pogonophores, hemichordates, and echinoderms. No phylum originated on land, and no major terrestrial taxon has become extinct, as far as is known.

Outstanding questions on terrestrialization are: what physiological mechanisms enabled invertebrates to emerge onto land; did each taxonomic group use similar mechanisms; were their routes onto land the same; did they all come onto land simultaneously, suddenly or gradually, or in different invasions? The hardest evidence comes from comparative physiology, but palaeontology has the power to test theories based on living material, and uniquely adds the dimension of time.

Invertebrates moving from seawater to land experience profound changes in all aspects of life (Little 1983). On land, water supply is at least variable, and commonly seasonal. To invertebrates, whose air breathing mechanisms utilize diffusion to a far greater extent than ventilation, oxygen is more available in air than in water because the diffusion coefficient (partial pressure per unit length, in ml/[min x cm^2 x cm × atm]) of oxygen in

water is 0.000034, but in air is 11.0. Support is more problematical in the less viscous aerial medium than in water, but once overcome, locomotion is easier and faster. The difference in refractive index between air and water poses a problem for visual sense organs in transition, but high frequency vibrations can be perceived more easily in air, resulting in a greater use of sound by terrestrial invertebrates. On land, internal fertilization is the norm, and greater protection (e.g. from drought) is afforded to the developing embryos. Changes in nutrition, ion balance regulation, and excretion are also necessary for terrestrialization.

Some land animals avoid the difficulties of water supply by living in soil interstitial water; strictly, such animals (e.g. protozoans, ostracodes, and nematodes) should not be regarded as terrestrial. Poikilohydry is used only by small terrestrial animals, such as protozoans, tardigrades, nematodes, and rotifers, whose habitat is subject to seasonal drought periods. Many soil, litter, and crevice dwellers are able to take advantage of the high humidity in such habitats, and though they are often able to foray in drier situations (e.g. woodlice across the kitchen floor), retreat to the humid home base is essential to prevent desiccation. In addition to woodlice, the centipedes, millipedes, flatworms, leeches, and earthworms are included in this group. Some animals, such as many land snails, can withstand desiccation during dry periods by aestivation, but require water or high humidity for activity at other times. Finally, the true invertebrate conquerors of the terrestrial habitat, not requiring a humid environment in which to flourish, but active in dry, and even desert, conditions, are the majority of insects, many arachnids, and a few crustaceans. All terrestrial arthropods have waterproofing in the cuticle, but the form this takes differs in each arthropod group and is not always well studied. The differences may be important for palaeontology, however, since the preservation potential for different cuticles is not the same.

The fossil record

The fossil record of terrestrial invertebrates is shown in Fig. 1 (Rolfe 1980; Chaloner & Lawson 1985). There is no fossil record of terrestrial flatworms, nemerteans, or nematodes, although fossil examples of parasitic and aquatic nematodes are known (Conway Morris 1981). Oligochaete annelids are known from the Carboniferous. Their traces, including burrows and faecal pellets, occur in palaeosols from the Carboniferous onwards. They may have emerged onto land with the first humic soil (Section 1.8.1).

Land snails, both helicinid prosobranchs and stylommatophoran pulmonates, are recorded from the Upper Carboniferous, indicating that they had already become significant members of the land fauna by that time. The earliest basommatophoran pulmonate is Late Jurassic in age; this contradicts evidence from comparative morphology, which suggests that basommatophorans were ancestral to the other pulmonates. Possibly the development of ground shade and deciduous leaf litter (probably Lower Carboniferous) was necessary before land snails could be assured of the damp conditions necessary for colonization (Solem 1985).

All extant insects are terrestrial or secondarily aquatic, and there were no terrestrial trilobites, as far as we know. The record of Onychophora, which includes the Recent *Peripatus*, appears to begin with *Aysheaia* from the marine, Middle Cambrian Burgess Shale. Terrestrial uniramians (myriapods and insects) were thought to have evolved from land-living onychophorans, but there is new evidence that the earliest myriapods were marine. This comes from myriapod-like fossils in marine sediments from the Silurian of Wisconsin and the Middle Cambrian of Utah. By the Devonian, millipedes, centipedes, and arthropleurids had appeared in terrestrial faunas, and some reached giant proportions in the Carboniferous forests. The earliest apterygote insects occurred in the Devonian, but the first pterygotes were Carboniferous in age.

Eurypterids ranged from Ordovician to Permian and were predominantly aquatic animals, but from the Silurian onwards some were amphibious, as evidenced by their accessory lungs. They illustrate a failed attempt at terrestrialization using a method now being tried by the Crustacea. Their close relatives, the scorpions, succeeded however, by changing their gills into lungs. All other arachnids are primarily terrestrial today, and the evidence from comparative morphology suggests that each arachnid group emerged onto land independently. The oldest are the trigonotarbids: extinct, close relatives of spiders, with good terrestrial features, from the Lower Devonian of Rhynie, Aberdeen. In the Devonian are also found mites, pseudoscorpions, and possibly spiders, and by the Carboniferous there were more arachnid orders than today; only the spiders have radiated more dramatically in later periods.

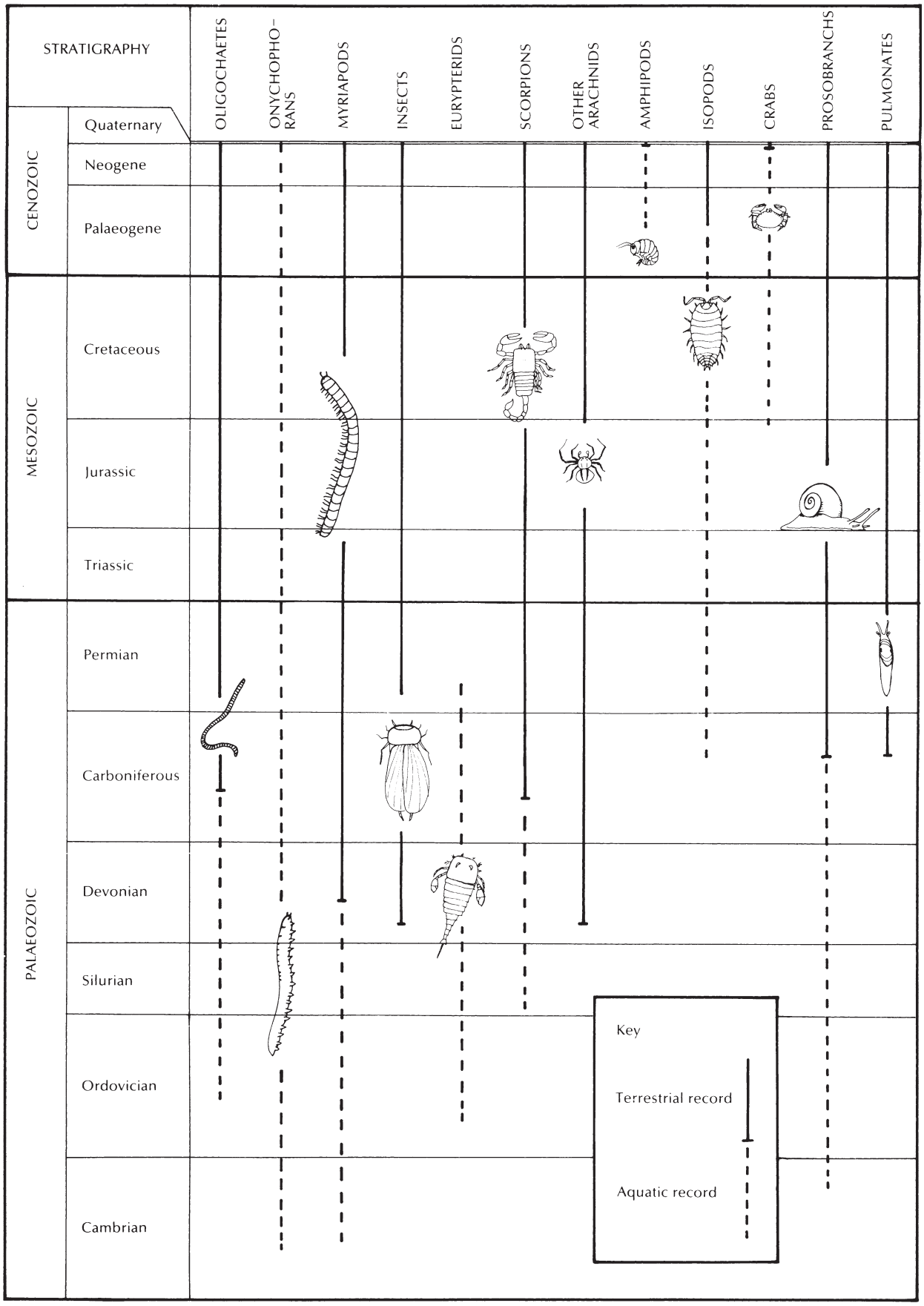

Fig. 1 The fossil record of terrestrial invertebrates and their forebears.

The fossil record of crustaceans is generally good because, like the trilobites, they have a mineralized exoskeleton. However, the terrestrial groups show very short fossil ranges. The first amphipods are Upper Eocene, although it has been suggested, on biogeographical grounds, that their origins lie in the Middle to Late Mesozoic at least. The terrestrial talitrids, with no fossil record, are considered by some to have emerged onto land when the first angiosperm forests became established in coastal regions. The isopods have a long fossil record, from the Upper Carboniferous, with their supposed origins in the Devonian, but the terrestrial Oniscoidea are known only since the Eocene. Although crabs and crayfish first appeared in the Jurassic, the important crab radiations did not occur until the Cretaceous and the Eocene; families with terrestrial representatives first appeared in the Palaeogene, but true terrestrial forms not until the Late Neogene.

Morphological adaptations for life on land

A major problem for terrestrializing animals is that both oxygen and carbon dioxide molecules are larger than the water molecule, so that any membrane across which the respiratory gases are diffusing will leak water. This may not be too disastrous in moist environments like the soil, in which animals such as earthworms can use cutaneous respiration, but inhabitants of dry habitats need a waterproof skin and have developed special respiratory organs to reduce water loss. Respiratory organs can be broadly classified into gills, (evaginations) used primarily in water and lungs (invaginations used primarily in air). A great many animals utilize cutaneous gas exchange in conjunction with gills or lungs. Aquatic animals which venture onto land for short periods of time may use their gills for air breathing, but if much time is spent on land, accessory lungs are usually developed. Many examples of animals with both lung and gill can be found among the gastropods and the Crustacea. In some instances, the lung developed not for land life, but to withstand poorly oxygenated water or drought periods (cf. lungfish).

True lungs among the invertebrates are found only in gastropod molluscs and arthropods. Among gastropods the pulmonates (land snails and slugs), and a few prosobranchs (e.g. helicinids), are the only truly terrestrial forms. The gastropod lung is formed from a highly vascularized part of the mantle cavity, which in pulmonates opens by a small pore (the pneumostome) to the outside. In the arthropods, book-lungs, tracheae, and pseudotracheae are all types of lung which have evolved independently in a number of groups. The book-lungs of arachnids are homologous with the gills of the aquatic chelicerates, and appear to have been derived from them simply by sealing the edges of the gill covers and leaving a hole (the stigma) to connect to the outside. The early scorpions (Silurian to Carboniferous) were aquatic and gills are known in the Devonian *Waeringoscorpio* from Germany; but by the Lower Carboniferous, pulmonate scorpions had appeared alongside the aquatic forms. In the related, extinct eurypterids, the so-called gills actually resemble some crustacean air-breathing organs, which suggests that this was their real function, and that true gills, being thin membranes, have not been preserved or recognized in fossils. As in the pulmonate gastropod lung, dendritic structures resembling insect tracheae have developed within the book-lungs of some arachnids; additionally, some arachnid groups have developed tracheal systems. Among the chelicerates, therefore, respiratory organs developed independently in each group by modification of various pre-existing organs according to need.

The insect tracheal system is a dendritic pattern of tubes arising from apertures (spiracles) in the body wall, and penetrating to every tissue in the body to supply oxygen directly to the cells. Since the insects appear to have evolved from terrestrial myriapods, the problems of terrestrialization have never troubled them, which may explain their success. A variety of tracheal systems occurs among the myriapod groups. Several independent terrestrial lines are found in the Crustacea (Powers & Bliss 1983), principally the talitrid amphipods, the isopods, and the land crabs. In the land crabs, secondary lungs are developed that work alongside the gills (which are never lost). The isopods are more terrestrialized than the crabs, and their pleopods (gills) bear invaginations (termed pseudotracheae, from their resemblance to insect tracheae) for air breathing.

For small animals, hydrostatic skeletons work as well on land as in water; witness the success of the slug form. Arthropods moving onto land evolved the hanging stance for stability, and additionally use some form of leg 'rocking' or jointing mechanism to prevent the plantigrade foot from twisting on the ground (with consequent abrasion and loss of grip) during walking; such features can be seen in fossils. Arthropods become vulnerable during

moulting, and it is possible that pioneer terrestrial forms returned to the water for ecdysis. Sense organs on fossils can give clues to terrestriality: trichobothria (fine hairs which respond to air vibrations) found on Devonian arachnids prove their terrestrial mode of life, and stridulatory organs on the same animals at least suggest it. Complex copulatory organs preserved in fossils suggest a terrestrial habitat and their absence is evidence for an aquatic life.

Routes onto land

The physiological barrier between sea and land can be crossed by a number of routes. Invertebrates which moved onto land across the marine littoral environment include the talitrids, the isopods, and most crabs, within the Crustacea, and possibly the chelicerates and the uniramians. There is evidence that some terrestrial forms emerged via brackish water (some crabs) or salt marshes (some pulmonate snails). The freshwater route was used by the oligochaetes, leeches, prosobranch gastropods, and the burrowing potamonid crabs and crayfish. Interstitial forms have utilized both fresh- and salt water routes, and it is possible that the very earliest land animals followed this route. Indeed, a late Ordovician palaeosol from Pennsylvania is full of coprolite-bearing burrows which have been attributed to the activities of microarthropods, possibly myriapods (Section 1.8.1).

From the fragmentary record, it would appear that most terrestrial invertebrates arrived on land with, or shortly after, the Silurian plant invasion (Section 1.8.2). The first records are of fully adapted land animals (the Rhynie Chert of Aberdeen, the Alken fauna of Germany, and the Gilboa fauna of New York), which points to a pre-Devonian terrestrialization period for most groups. The major exception is the Crustacea, which are attempting terrestrialization now. The pressures, or advantages, which cause terrestrialization are undoubtedly various (e.g. escape from predators, more abundant food supply) and invite speculation. What is clear, however, is that animals came onto land together with their biotic interactions, and hypotheses should seek to explain the invasion of the land by biotas rather than individual taxa.

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1.8.4 Vertebrates

A. C. MILNER

Introduction

The earliest terrestrial radiation is presumed to have been of fish-like tetrapods (four-legged land vertebrates — amphibians, reptiles, birds, and mammals) capable of moving on land and breathing air. Modification of structure, function, and physiology in subsequent radiations led to a monophyletic group of truly terrestrial vertebrates, the amniotes. The amniotes comprise two sister groups: theropsids, which include mammals; and sauropsids, which include reptiles and birds. Amniotes evolved a totally terrestrial life cycle, eliminating an independent aquatic larval phase by means of a relatively waterproof extraembryonic membrane (amnion) which encloses the developing embryo in fluid, and a shelled egg. This reproductive strategy enabled colonization of the terrestrial environment, and early amniotes diversified into lineages leading ultimately to mammals and birds.

The earliest tetrapod record

Tetrapod remains first appear in the fossil record in the Frasnian stage of the Upper Devonian. The only abundant skeletal remains are those of the ichthyostegalians, discovered in the nineteen-thirties in the Famennian red beds of East Greenland (Jarvik 1980). Three genera have been recognized, *Ichthyostegopsis*

from skulls only, and *Acanthostega* and *Ichthyostega* from skull and postcranial material, although no complete skeleton has been described (Fig. 1). *Ichthyostega* is undoubtedly the most primitive tetrapod known and retains many fish-like characters. Specialized autapomorphies debar it from direct ancestry of all other tetrapods.

Tetrapod–fish relationships

The orthodox view of the origin of tetrapods is that they derive from one particular group of bony fishes (Osteichthyes), the osteolepiforms, which are all fossil. This is currently in dispute and the subject of major contradictory reviews. Rosen *et al*. (1981) have argued that lungfish (Dipnoi) are the sister group of tetrapods, based on the shared derived character of a choana (internal nostril) and other supporting homologies. Panchen and Smithson (1987) reappraised the same data and concluded that lungfish do not share a true tetrapod choana; they support the traditional view that osteolepiform fishes are the sister group of tetrapods and, therefore, that the extinct taxa contained in that group are more closely related to tetrapods than are the lungfish.

Both osteolepiforms and dipnoans first appear in the Lower Devonian and if either is the sister group of tetrapods then the earliest tetrapods must also have been present in the Lower Devonian (Bray 1985; Milner *et al*. 1986). It is now generally accepted, however, that the tetrapods are monophyletic. A diphyletic origin from two separate groups of fossil osteichthyan fishes has been proposed by Jarvik (1980). His theory derives living urodeles (salamanders) from porolepiforms, and all other tetrapods (amphibian and amniote) from osteolepiforms; it has not received support outside the Swedish school.

Morphological adaptations for life on land

The classical scenario painted a picture of terrestrial vertebrates emerging onto land from freshwater, argued on physiological grounds. Such a transition was thought to be in response to periodically arid environments, as interpreted from the sedimentology of the Devonian red beds. Recently, a number of authors (references in Bray 1985) have argued that the geological evidence favours a marine origin both for vertebrates as a whole and for tetrapods. Devonian osteichthyans are mainly associated with marine or nearshore continental environments and, indeed, the ichthyostegalians may be associated with coastal tidally-influenced sediments (Bray 1985).

Air breathing, by means of internally positioned inflatable airsacs with moist linings (lungs), is a basic character for osteichthyan fishes found also in tetrapods. It may also have been, primitively, an adaptation to the marine environment for all jawed fishes (gnathostomes) (Bray 1985). Ureotelic nitrogenous excretion (production of urea to minimize osmotic dehydration) is found primitively in marine vertebrates. Thus two important physiological adaptations to the terrestrial environment, air breathing and the ability to cope with dehydration, were already present in the osteichthyan fishes from which tetrapods evolved.

An alternative and completely opposite scenario then, is that the environmental pressures leading to terrestrialization might have been the drive to escape from freshwater influx (and the inherent physiological problems of maintaining water

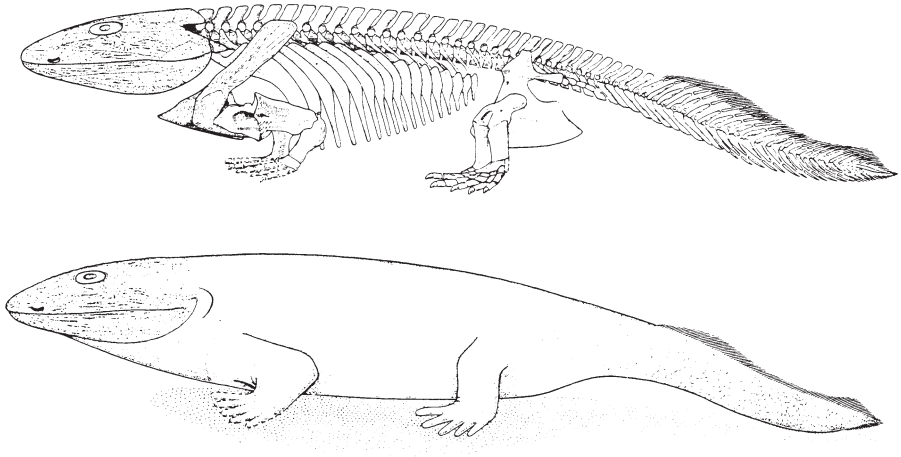

Fig. 1 Composite skeletal reconstruction and flesh restoration of *Ichthyostega*, the most primitive terrestrial tetrapod known. Length about 65 cm; the largest specimens attained a length of about 1 m. (From Jarvik 1980.)

balance in hypo-osmotic conditions) into shallow marine environments during a wet season (Bray 1985).

Major structural and functional adaptations are implicated in the terrestrialization of vertebrates, among them modifications of the systems involving movement and support, sensory perception, and reproduction.

A complex of limb and limb girdle characters, autapomorphic for tetrapods (Rosen *et al.* 1981; Panchen & Smithson 1987) reflect the interwoven functions of supporting body weight and transmitting muscular locomotor forces to the distal regions of the limbs. *Ichthyostega*, which inevitably serves as the primitive tetrapod model, displays the following characters which demonstrate the acquisition of fully functional walking limbs and sprawling gait (Jarvik 1980): pelvic girdle connected to the vertebral column; form of the jointed limbs with a hinge joint at the wrist and knee and a rotary ankle joint; and load bearing digits with articulated phalanges (Fig. 1). The derivation of the tetrapod limb from the fin skeleton of either a lungfish, as argued by Rosen *et al.* (1981), or an osteolepiform, preferred by Panchen & Smithson (1987), presents complex problems of homology which cannot be resolved satisfactorily from the present fossil record.

The ability to receive airborne sound is an important adaptation to life on land. Tetrapod autapomorphies in the middle ear, namely the presence of a fenestra ovalis in the otic capsule (part of the braincase housing the semicircular canals of the inner ear) and a stapes (an unsutured rod-like bone providing a connection between the otic capsule and the body wall) indicate that early land vertebrates were able to receive low frequency airborne or water-borne sound. Structural adaptations to receive and process high frequency sound, with a slender stapes acting as a sound conductor in an impedence-matching middle ear, had developed by Visean times in temnospondyl amphibians (from which modern amphibians derive). An impedence-matching middle ear developed independently in amniotes and is observed first in some Permian forms.

The configuration of the ear region offers clues to the evolutionary transition from amphibians to reptiles (i.e. amniotes). Soft structure autapomorphies are not reflected in the skeleton of early land vertebrates that were related to amniotes; they cannot be categorized satisfactorily on skeletal characters. The relative size of the semicircular canals (organs of hearing and balance in the inner ear), proportionally much larger in small animals, led Carroll (1970) to propose that the transition from an amphibian (non-amniotic) to a reptilian (amniotic) reproductive pattern occurred through a filter of small adult body size. Reproductive patterns of living terrestrial amphibians suggest that there was an intermediate stage in the development of terrestrial reproduction when non-amniote eggs were laid on land. Non-amniote eggs are restricted in size for physiological reasons, imposing in turn a strict limit on adult body size (Carroll 1970). It is also a recognized reproductive strategy for small terrestrial amphibians to produce a small number of relatively large yolky eggs. This permits the offspring to reach an advanced stage before hatching and is a more efficient energy investment in small forms. Whatever the underlying cause, the process of miniaturization involved remodelling of the skull and braincase to accommodate the still relatively large semi-circular canals. Thus the structure of the ear region is fundamentally different in amniotes and anamniotes.

The earliest tetrapod that can be unequivocally characterized as an amniote, *Hylonomus*, is Westphalian (Middle Silesian) in age. It possesses a suite of characters highly adaptive for a fast-running small insectivore, including slender limbs and long, slender manus (hand) and pes (foot). It might therefore be concluded that this condition represents the primitive amniote ecological niche. However, a recent review of early amniote relationships concluded that the early amniote ecological niche was filled by small, slow-moving general invertebrate feeders (Heaton & Reisz 1986). There is a striking correlation between the appearance of slenderly-built cursorial insectivores, exemplified by *Hylonomus*, in the late Carboniferous and the increasingly diverse fauna of running and flying insects.

Early tetrapod biogeography and ecology

In addition to the ichthyostegalians, the geographical range of Devonian forms has been extended recently by discoveries of tetrapod footprints from the Frasnian Stage in Australia and from the Upper Devonian in Brazil. A possible tetrapod lower jaw is also known from Australia and a partial skeleton, unequivocally tetrapod and more advanced than the ichthyostegalians, has recently been described from the Upper Famennian of European Russia (Milner *et al.* 1986). The Upper Devonian tetrapod

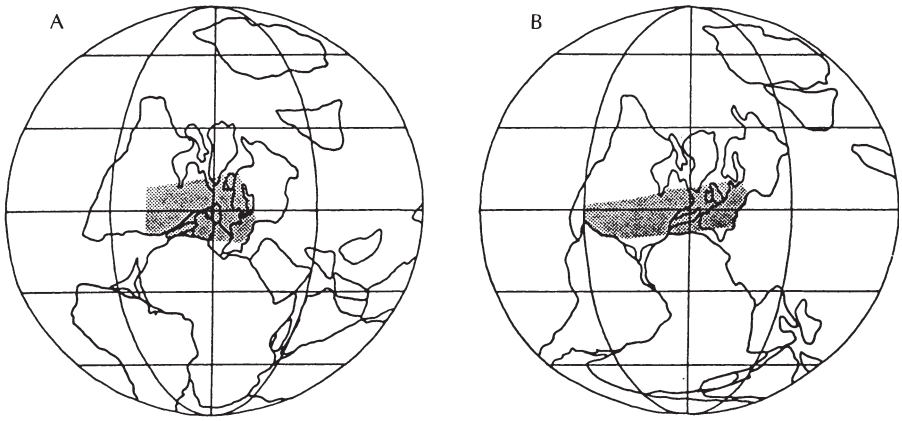

Fig. 2 The world in A, Tournaisian–Namurian and B, Westphalian time, showing the known range of fossil tetrapods (stippled) in relation to contemporaneous continental positions. (After Milner *et al.* 1986.)

record is thus very sparse; it demonstrates that tetrapods were present by the late Devonian in the palaeoequatorial regions of Euramerica and Gondwanaland but information on structural and ecological diversity is lacking.

Our knowledge is likewise restricted geographically and ecologically during the Carboniferous. For discussion of the tetrapod record, the Carboniferous is most usefully divisible into two coherent units (Milner *et al.* 1986). In the Tournaisian/Visean/Namurian (360–315 Ma) most of the dozen or so families recognized are of large specialized aquatic forms, and a few specimens of small terrestrial tetrapods hint at almost unrepresented terrestrial faunas. All the tetrapods known from this period occur in a band across the southern coastal region of Euramerica from Iowa to West Germany (Fig. 2A) and most derive from lake-bed or estuarine deposits, hence the predominance of specialized aquatic forms. A recently discovered Scottish Dinantian terrestrial fauna (Milner *et al.* 1986), albeit very late Visean in age, is revealing a wider structural diversity among terrestrial tetrapods and increases the probability that they were already structurally and ecologically diverse in the late Devonian.

All Westphalian tetrapod faunas known, with the exception of one trackway recorded from the late Carboniferous of Chile, also derive from the southern margin of Euramerica in a slightly wider longitudinal belt from Arizona to Czechoslovakia (Fig. 2B). Some 30 families are recognized, apparently an explosive increase in diversity compared with the pre-Westphalian record. However, this phenomenon is an artifact of the existence of a few highly productive Westphalian localities which represent three major environments and tetrapod associations (Milner *et al.* 1986). These are: (1) an open-water fish-dominated habitat with specialized lake dwelling tetrapods; (2) a swamp pool association, a pond-like environment where small amphibians predominated but with occasional lake and terrestrial erratics; and (3) terrestrial associations found as erratics in swamp pools, deltaic fans or as the major assemblages in burnt hollow upright lycopod stumps. This last preservation, from sites in Nova Scotia, has yielded remains of small animals that had been either entrapped or used the stumps as refuges. These animals show obvious terrestrial adaptations and they include the earliest known reptile, *Hylonomus* (Milner *et al.* 1986).

It is evident from the above brief survey that virtually all that is known of the first quarter of tetrapod history (374–296 Ma) derives from an apparent succession of faunas in a geographically restricted area — the southern equatorial coastal belt of the Euramerican plate. This has been interpreted variously as the centre of origin and diversification of terrestrial vertebrates, and as the result of a concentration of collecting activity in Europe and North America. Likewise it appears, from literal interpretation of the fossil record, that the origin and early radiation of terrestrial vertebrates was a chronological sequence of faunas evolving in response to environmental changes. The record may equally represent local succession of ecological communities along the southern coast of Euramerica. The poverty of the fossil record in the Devonian and Carboniferous severely restricts our perspective on these problems.

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1.9 Flight

1.9.1 Arthropods

R. J. WOOTTON

Introduction

Although mites and small spiders are frequently carried passively by air currents, insects are the only arthropods to have developed the power of active flight. Flight had already evolved by the early Namurian, when insects first appear in the fossil record. Namurian insects are rare, but Westphalian deposits — in particular the spectacular beds of Mazon Creek, Illinois (Westphalian C–D) (Section 3.11.5) — display large, developed faunas of winged insects, diverse enough to indicate that flight may have arisen by the end of the Devonian. A handful of primitively wingless (apterygote) Carboniferous insects are known; but there are no convincing 'protopterygotes' to indicate the nature of the transition — leaving ample scope for speculation.

Debate has focused on two areas: the homology, nature, and functions of wing precursors; and the circumstances and means by which flight arose.

The homology and functions of the pro-wings

Two hypotheses, both with their roots in the 19th century, are still in contention:

1 The paranotal lobe theory maintains that wings arose by enlargement of the second and third thoracic pairs of a segmental series of fixed, flat dorsolateral outgrowths, the paranotal lobes. Supporting evidence is provided by the presence of such lobes on the first thoracic segment and sometimes the abdominal segments of adult Palaeozoic insects in several orders (Fig. 1A), of a few later and extant forms, and of several Carboniferous nymphs in which the wing pads appear as part of a continuous series of lateral lobes on thorax and abdomen (Fig. 1B). This was the orthodox view until the late nineteen-seventies and is still widely supported, sometimes in a modified form (Rasnitsyn 1981; Quartau 1986).

2 The tracheal gill theory, revived by Wigglesworth (1976) and developed by Kukalova-Peck (1978, 1983), claims that wings are homologous with the abdominal gills of juvenile mayflies (Ephemeroptera), and that both are ultimately derived from articulated projections of ancient basal leg segments, now incorporated into the sides of the body. Kukalova-Peck has quoted considerable supporting evidence from fossil and extant insects, including Carboniferous and Permian mayfly nymphs with strikingly wing-like gills (Fig. 1C). The theory, though by no means universally accepted, has now to be taken seriously.

There is an important distinction between the two hypotheses. In the paranotal theory the lobes are presumed to have been immovable, and only later to have developed a mobile articulation with the thorax, as flapping flight evolved. In the tracheal gill theory the wing precursors are seen from the first as actively movable appendages whose form, articulation, and musculature altered progressively with their functions. Movable or not, the forerunners of wings would not have begun to generate useful aerodynamic forces until they had reached a certain size and shape, and it is necessary to find

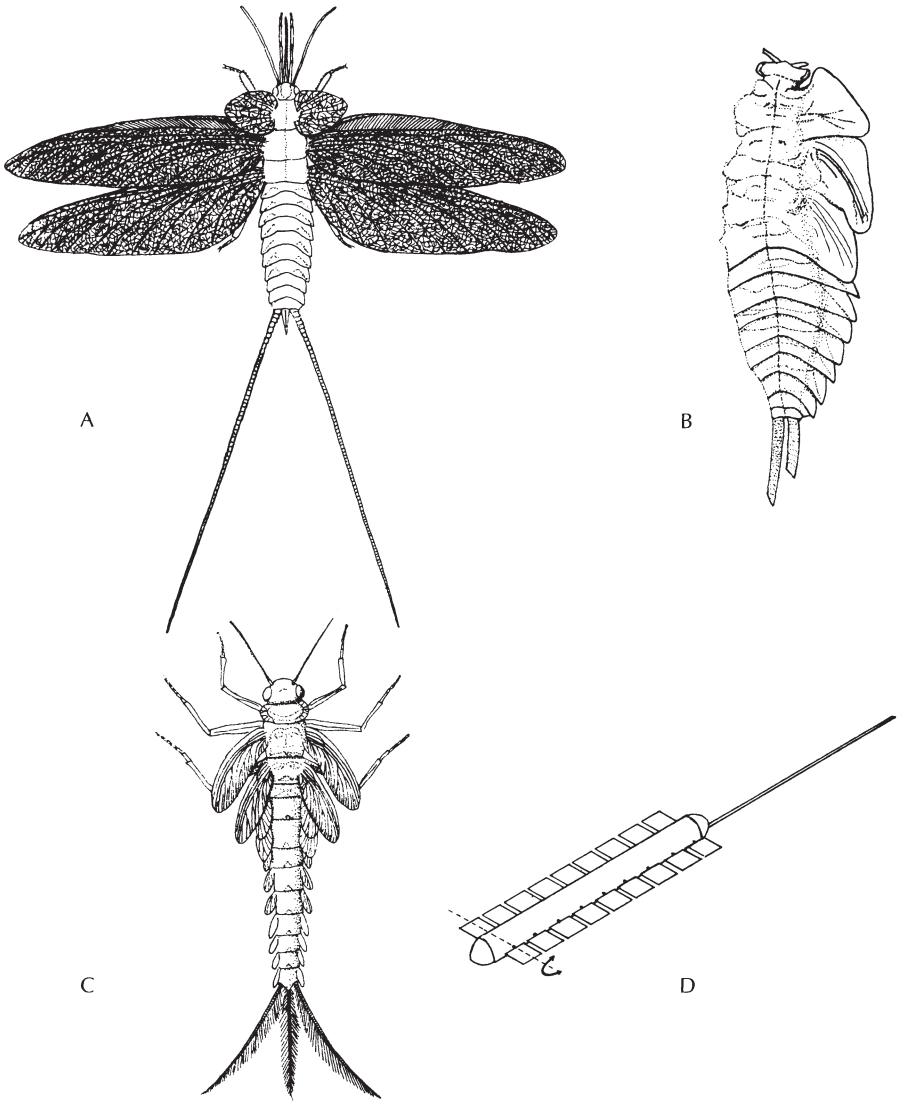

Fig. 1 A, *Stenodictya* (Order Palaeodictyoptera), reconstruction based on several species. Body (minus cerci and mouthparts) *c.* 60–70 mm long. (After Kukalova 1970.) B, *Rochdalia parkeri* (Order Palaeodictyoptera), nymph. Upper Carboniferous. Length (excluding cerci) 22 mm. (After Wootton 1972.) C, *Kukalova americana* (Order Ephemeroptera), nymph. Lower Permian, Oklahoma. Length 21 mm. (Reconstruction after Hubbard & Kukalova-Peck 1980.) D, Balsa model, as tested by Wootton and Ellington (1991). Lengths 80 mm and 160 mm. The winglets could be twisted around their mounting to alter the angles of attack.

some earlier functions to account for their reaching this stage.

Fixed lateral lobes — most of them certainly not homologous with wings — occur in many modern insects, particularly in juveniles. They act variously: to streamline sedentary aquatic insects pressed to a substrate; and in several kinds of defence — in mimetic camouflage, as armament, or to obscure outlines or reduce shadows. All these have been suggested as possible pro-wing functions. A recent candidate is thermoregulation. Kingsolver and Koehl (1985), experimenting with model insects of three sizes equipped with several sizes of thoracic winglets, found that the latter increased heat uptake — up to a certain size beyond which no further effect could be detected. This size corresponded well with that at which aerodynamic effects became detectable in wind tunnel experiments. In the authors' view pro-wings developed as thermoregulatory structures, and were so preadapted for flight.

The functions proposed for the forerunners of wings in the tracheal gill hypothesis are more straightforward. The basal segments of the legs of modern apterygote insects bear articulated styles, homologous with neither gills nor wings but similar in form to those envisaged as early wing precursors. Their function is sensory. The flattened plate-like gills of many mayfly nymphs serve in gaseous exchange and can usually be flapped, increasing the rate of water flow over the body and providing ventilation, and in some cases propulsion.

Gills are aquatic adaptations, whereas wings function in air. All variants of the tracheal gill theory

assume that the ancestors of winged insects were aquatic or semiaquatic, at least as juveniles, and that the gills persisted in forms which became terrestrial, at least as adults. Rather inconveniently for this theory, extant apterygotes are predominantly terrestrial; but there is no reason why protopterygotes should not have evolved by way of a secondarily aquatic line. The adoption, or readoption of terrestrial habits then needs to be explained. Wigglesworth (1976) and Kukalova-Peck (1983) proposed that aquatic or semiaquatic protopterygotes took to climbing up emergent or waterside vegetation, perhaps to feed on the energy-rich sporangia, and so became available for aerial dispersal.

The development of flight

The many theories which have been put forward on the circumstances of the origin of flight fall into three groups. Variants of each were current when the paranotal lobe theory held exclusive sway, but some recent versions take account of the new factor of pro-wing mobility inherent in the tracheal gill hypothesis:

1 The running/jumping theory. Protopterygote insects gained the speed necessary for flight by running or jumping into the air, perhaps to escape from predators, and planed or flapped to a landing.

2 The floating theory. Flight evolved in insects small enough to be carried up by winds or thermals. Pro-wing enlargement was favoured by selection for high surface/volume ratio, and thus high drag.

3 The parachuting/gliding theories. Arboreal insects falling or jumping from a height used their pro-wings initially for parachuting, then progressively for gliding and powered flight.

In each hypothesis it is assumed that selection for improved aerodynamic efficiency led to the enlargement of the pro-wings on the second and third thoracic segments, and to the reduction and eventual loss of the remainder; and that performance was further enhanced by the development or improvement of the power of flapping, with its associated morphological and physiological adaptations.

One theory can be ruled out. Running and planing over level ground would be pointless, since even if take-off speed were reached the insect would begin to slow down as soon as it left the ground. Choice between jumping, floating and paragliding is a matter of estimating relative probabilities. The hypotheses are not entirely mutually exclusive — an insect jumping from an eminence into rising air would have features of all three — but their implications are rather different.

The jumping theory requires that a protopterygote with a small pro-wing area could generate enough lift, with or without flapping, to achieve useful, stable, shallow flight, within the speed range which could be reached in a leap.

The floating theory implies that an insect small enough to be carried by air currents would develop the morphological characteristics appropriate to powered flight.

The parachuting/gliding theories require that pro-wings should initially maintain the insect in a stable attitude which would enable it to generate some lift in falling, and so glide or fly to a lower level slowly enough to avoid being damaged in landing.

Several of these criteria have been investigated by Wootton and Ellington (1991), by dropping appropriately scaled cylindrical balsa models with serial winglets which could be rotated to particular angles relative to the body axis (Fig. 1D), so testing the effects of one aspect of pro-wing mobility. They found that models scaled to be dynamically similar to an insect *c.* 25 mm long parachuted stably and relatively slowly at steep glide angles, if the winglets were rotated backward so as to be fully stalled at angles of attack around 85°, but were incapable of shallow glides. However, larger models corresponding to insects *c.* 70 mm long — well within the size range of Palaeozoic forms — were capable of fast shallow glides, the speed and angle of which could be adjusted by minor changes in the angle of attack of the winglets. Removal of 'abdominal' winglets destroyed stability in the pitching plane, but this was readily restored by adding slender tail filaments, such as are found in many primitive winged insects (Fig. 1A).

These results appear to favour the parachuting/gliding hypothesis, since shallow glides only proved possible at speeds well in excess of those normally achieved in a jumping take-off; a period of acceleration in free fall is needed. The evidence also indicates that the ability to change the angle of attack of the pro-wings would have been valuable in controlling glide angle and speed, and perhaps in ensuring stalled soft landings. Preliminary unpublished calculations suggest that flapping would have had negligible effect on flight performance in the

early stages of flight evolution, but would have become increasingly effective as the pro-wings enlarged in association with improved gliding.

The evolution of powered flight from passive floating is far harder to envisage. Selection for drifting efficiency might favour the enlargement of body appendages, but with a high-drag morphology which would not adapt them for active flight. Selection would, however, favour small size, which would necessitate uncomfortably high flapping frequencies even when the wings had become fully developed. The advantages of flapping at the pro-wing stage would be infinitesimal.

Conclusion

Recent discoveries notwithstanding, hard information on the origin of insect flight is still rather scarce. On balance, the combined evidence from palaeontology, comparative morphology and experimental biomechanics suggests that flight probably evolved in the Devonian, in medium to large arboreal insects initially bearing serial lateral appendages which may have been capable of being actively twisted, and perhaps flapped. The appendages may at first have served to stabilize and slow the insects' falls, but came to provide lifting surfaces, allowing shallow fast glides. There followed enlargement of the winglets closest to the centre of mass, to a size where flapping became effective in generating thrust and weight-support; and reduction of the remaining winglets, accompanied by enlargement of caudal appendages to prevent loss of stability.

Though in no way proven, a scenario of this kind is both feasible and fairly parsimonious. No evolutionary 'quantum leaps' would be required. Given the initial presence of small articulated lateral appendages, the insects could pass from winglessness to active flight by gradual stages, all of which make functional sense.

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1.9.2 Vertebrates

K. PADIAN

Introduction

Three groups of terrestrial vertebrates have evolved flight independently: pterosaurs (Late Triassic–Late Cretaceous), birds (Late Jurassic–Recent), and bats (Eocene–Recent). By 'flight' is meant flapping flight; parachuting, gliding, and soaring are other, different modes of flight. Parachuting is descent slowed mainly by drag; in gliding, lift predominates and the angle of descent tends not to exceed 45°. Soaring, as opposed to these two passive modes of flight, actively uses the energy of rising thermals and air currents to maintain height, even though the wings are fixed. Soaring habits seem to have evolved only in active flyers, not in passive ones, although aerodynamically there seems to be no reason why passive flyers could not soar; however, their wings are not long and narrow like those of other soarers.